

Observations of the Sound Production Capabilities of the Bottlenose Porpoise: A Study of Whistles and Clicks¹

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(Plates I-IV; Text-figures 1-6)

INTRODUCTION

FOR centuries man has been aware that of all the creatures of the sea the whales and porpoises are among the most vociferous. Recent research (Norris *et al.*, 1961; Kellogg, 1958; Kellogg, *et al.*, 1953) has demonstrated that one functional aspect of this vocal behavior is its use in navigation and food-finding by the process of echo-location. This form of behavior has proved to be particularly interesting to laymen and the military as well as psychologists and zoologists, and it is not surprising that the other vocalizations produced by these animals have been relatively neglected. That they have the ability to emit several sounds in addition to those used for echo-location raises the possibility that other functions, *e.g.* communication, are involved.

The best known cetacean is the Atlantic bottlenose porpoise, *Tursiops truncatus* (Montagu), but before a total and accurate description of the complex acoustic behavior displayed by this species can be drafted, a great many more data are needed. At present, information is available on the frequency range, duration and directionality of the signals it uses for echo-location. Some aspects of the swimming behavior associated with this activity have also been described (Norris *et al.*, 1961). On the other hand, little is known about the mechanisms used by the porpoise to produce its wide array of vocal signals, and the range and variability of the animal's

non-echo-location acoustic output has not been specified.

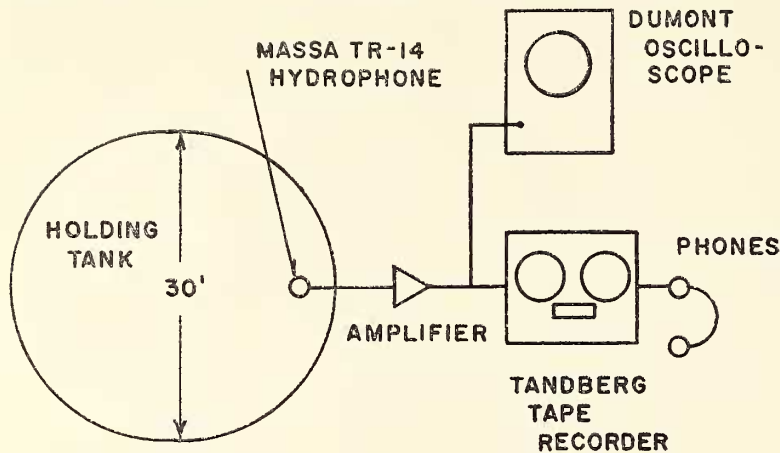
This paper describes some preliminary efforts to investigate the sound production apparatus and signal repertoire of the Atlantic bottlenose porpoise. The animals and facilities were made available through the cooperation of Marineland of the Pacific, where all observations were made.

We would like to express our gratitude to Mr. Wm. F. Monahan, Marineland of the Pacific, to Dr. John Dreher and Mr. William Sutherland, Lockheed Aircraft, and to Dr. Carl George, American University, Beirut, Lebanon, for their able assistance. We also wish to thank Mrs. Muriel Johnson for help in the preparation of the manuscript.

COLLECTION OF PORPOISE VOCALIZATION DATA

To initiate this investigation it was necessary to acquire an adequate sample of the vocal behavior of *Tursiops*. This was achieved by recording the sound production of a group of five to eight specimens which were confined in a concrete holding tank, 30 feet in diameter and 5 feet deep. Recordings from a single animal confined in a plastic-lined holding tank, 30 feet in diameter and 4 feet deep, were also obtained. In all, some six hours of taped data were collected during several recording sessions. A block diagram of the instrumentation used is presented in Text-fig. 1. The over-all response of this recording system was from 100 cps to 17 kcps, plus or minus two decibels, and the sensitivity was down less than 12 db at 20 kcps, with a tape speed of 7½ inches per second. The equivalent

¹Contribution Number 15, Marineland of the Pacific Biological Laboratory.



TEXT-FIG. 1. Block diagram showing instrumentation used to record porpoise vocalizations.

frequency response of the system at the reduced playback speed used for analysis, which was 3.75 inches per second, did not suffer, but was approximately one decibel better than that of the recording system.

The system used for the data analysis consisted of the tape recorder and a Sona-Graph sound spectrograph (Kay Electric Co., Pinebrook, N. J.). This instrument analyzes a complex signal as a function of time and frequency. The resultant portrayal, known as a sonagram, displays frequency along the vertical axis, time along the horizontal axis and intensity by the darkness of the pattern. The use of this type of equipment for the analysis of biological sounds has been thoroughly reviewed in Lanyon & Tavolga (1960).

Analyses of the recorded data indicated that all of the sounds produced by the animals fell into one of the following three categories.

(a) Clicks or plosive sounds—echo-location pulses with a time duration of .001 to .01 second and a frequency range 100 cps to 35 kcps and beyond. Although the recording equipment used in these studies has an upper frequency response limit of 20-24 kcps, it is adequate for studying certain aspects of the echo-location clicks. The echo-location signal may have its greatest intensity in the 20-35 kcps range; however, it appears in several regions of frequency reinforcement with considerable energy from 3 kcps to 20 kcps, which is within our recording range. We were thus able to determine and track pulse rate, frequency shift and other physical data of the echo-location clicks by utilizing the portions of the signal of lower frequency (below 22 kcps).

(b) Whistles—frequency modulated signals, very narrow band with one or two overtones; frequency range 4,000 to 20,000 cps.

(c) Barks—sounds rich in overtones which

must be produced in a system of complex resonators, frequency range 200 to 16,000 cps. Sonagrams showing a frequency *versus* time display for each of these types of sound emissions are presented in Plate I.

Sounds associated with echo-ranging were the most frequently observed acoustic phenomena. The animals were constantly echo-ranging the tank, checking for possible environmental change, *e.g.*, the addition of food. Repetition rates of this type of signal varied from one or two pulses per second to rates as high as 525 pulses per second.

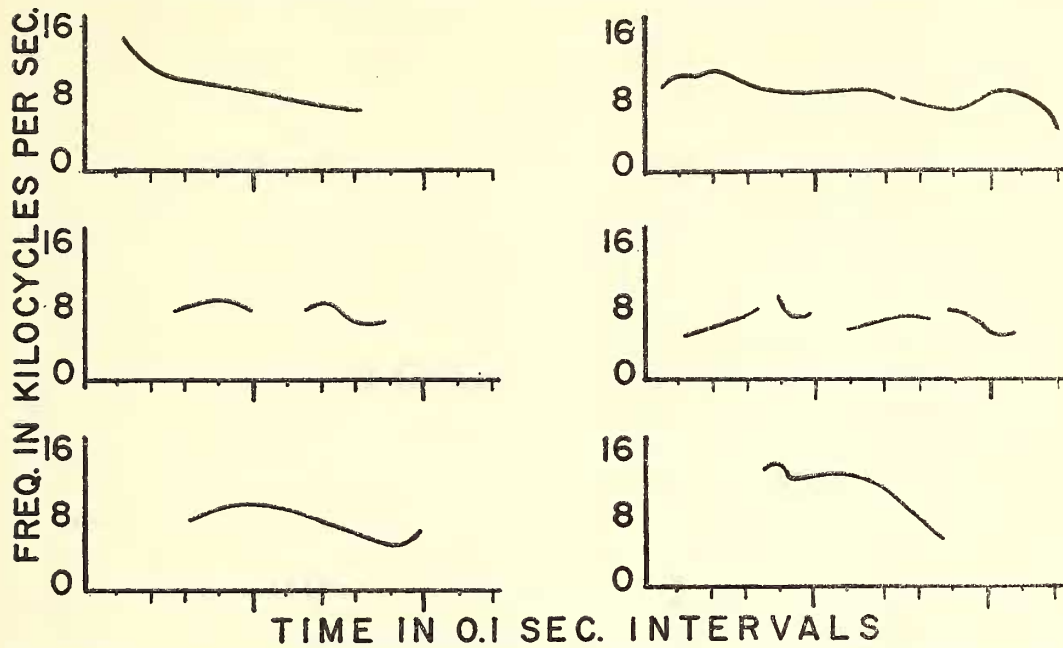
The next most frequently observed sounds were whistles. These whistles were usually associated with movement of one or more animals about the tank. The lowest frequency observed was 3.7 kcps and the highest about 20-22 kcps, with the signal durations varying from .10 to 3.6 seconds. The shape of the whistle contours were quite variable. In all, a total of 18 basically different whistles were observed. Stylized frequency *vs.* time plots of some of the most frequently observed whistles are presented in Text-fig. 2.

Barks were the most infrequently observed sound. The fundamental frequency of these signals varied between 200 and 300 cps with harmonics as high as 16 kcps. Signal duration was usually about 0.10 second. These barks usually occurred when the animals were engaged in some stationary activity rather than swimming.

MECHANISMS FOR SOUND PRODUCTION

Anatomical examination of the nasal and laryngeal tracts of the delphinids *Tursiops truncatus* and *Stenella graffmani* reveals structures that appear to be suited for the production of each of the sounds previously mentioned.

For the production of clicks (plosive echo-

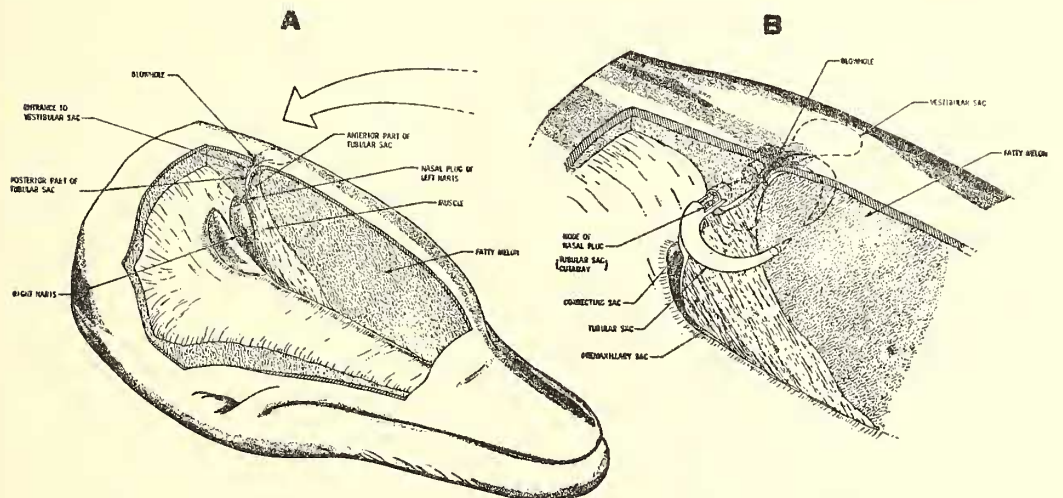


TEXT-FIG. 2. Composite diagrams showing frequency vs. time plots of six of the most frequently occurring whistles produced by *Tursiops truncatus*.

location sounds), the complex nasal sac system described by Lawrence & Schevill (1956) appears to be the most likely source. This system represents an interconnecting pneumatic tract with several *cul de sacs*, valves and lips.

The nasal sacs comprise the distal part of the nasal airway and lie within the soft tissues of the head, dorsad of the bony nares and premaxillary

bones of the skull (Text-fig. 3). They are located slightly below the fatty and connective tissue of the melon, or forehead, surrounded by their own muscle groups. All of them are paired. The premaxillary sacs are the largest and lie immediately on top of the smooth premaxillary bones, immediately anterior to the distal openings of the bony nares. The premaxillary sacs



TEXT-FIG. 3. Sketch of a bottlenose porpoise head with a cut-away exposing the naso-laryngeal tract, indicating the approximate locations of the nasal sacs, fatty melon and bony nares. A. Cutaway of whole head. B. Expanded view of sac system.

communicate with the bony nares, their soft posterior wall continuing as an extension to become the nasal plugs. The vestibular sacs are the outermost pair and lie posterolateral to, and just below, the lips of the blowhole. As Lawrence & Schevill (1956) have pointed out, "There is a considerable mass of tissue lying between the vestibular area and the dorsal surface of the plugs and it is here that the last two pairs of sacs, the tubular and the connecting, lie embedded. These are both true sacs in the sense that they are distinct from the main air passage and connect with it only via rather small, well marked openings." The tubular sacs are U-shaped with a slit opening in the lateral portion connecting to the main airway. They lie nearly horizontal in the head, almost surrounding the main airway. The connecting sacs are appendices to the tubular sacs and provide the only direct passageway for air from the tubular into the premaxillary sacs and then the main airway. These connections are along the distal edges of the nasal plugs near the base where the premaxillary sacs join the airway and open into the bony nares. Near the top part of the nasal plugs, at a point opposite the slit openings of the tubular sacs, there are small tongue-like nodes. Each of these appendages is inserted into the opening of the tubular sac (Text-fig.3). The intrinsic muscles appear to function as mechanisms to distend the tubular sacs, and transverse ligaments beneath the posterior limbs of the tubular sacs help stiffen the posterior walls of the passage (Lawrence & Schevill, 1956). These interconnections and other structures provide a passage for communication between the main air passages and the tubular sac. Such an arrangement links these sacs with the nasal airway without disturbing the position of the nasal plug and breaking the water- and gas-tight seal of the blowhole. It seems from examination of the musculature, the surrounding connective tissue and the lips of the tubular sacs that these mechanisms are capable either of maintaining or accepting the air pressures necessary to generate high frequency echo-location clicks. When air flows past the nodes of the nasal plugs projecting into the tubular sac, these nodes could vibrate, acting as a type of "raspberry" generator. This arrangement is not unlike the human tongue, inserted between the lips, used in producing a "Bronx cheer."

If the lens-shaped fatty body, or melon, characteristically found in the "forehead" of toothed whales could function as a variable focus "acoustic lens," then the complex nasal sacs and the accompanying pneumatic valve system would be ideally positioned. In light of Reysenbach de Haan's (1956) observations that blubber and fatty tissue are essentially acoustically

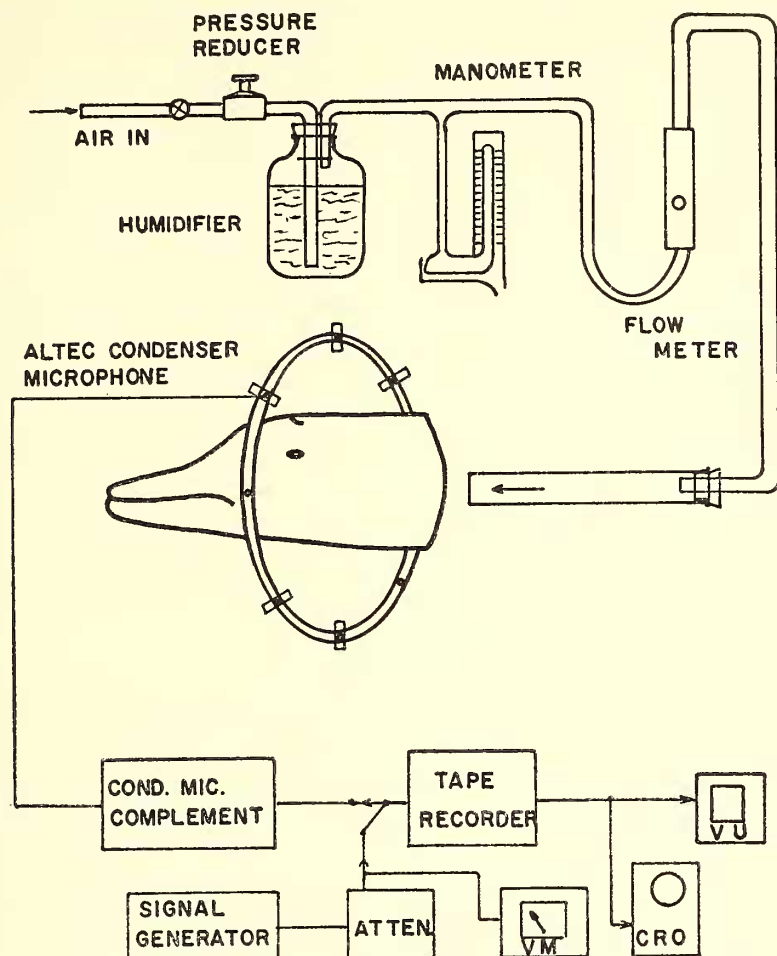
transparent due to their excellent impedance match for water, this arrangement would allow little energy loss of the air-produced sounds when transmitted into the water. Further evidence for this system exists in the somewhat modified asymmetric parabolic reflector formed by the dense bone of the premaxillae. Thus an acoustic lens, the melon, backed-up with the specially modified skull, could act to "focus" the animal's echo-location signals. The observations that when completing echo-location searches, in order to find targets or pick up food, *Tursiops* bends its head in a rapid circular scanning motion and appears to point its melon in the direction of search indicate that the sound pulse used is generated in the nasal sac system (Kellogg, 1960). Norris *et al.* (1961) noticed that a blind-folded *Tursiops* had difficulty in echo-locating objects positioned on a line below the melon.

Although the literature suggests that the Odontoceti have no vocal cords, as they exist in man for example, their larynx is a complex structure. The larynges of *Tursiops* and *Stenella* are shown in Plate II. Structurally, these larynges differ from those of terrestrial mammals in the elongated arytenoid cartilages and the accompanying epiglottic cartilage which form the aryteno-epiglottid tube. From the standpoint of structure alone, this smooth-surfaced, hard backed and constricted tube does form an ideal sound generator. For almost one hundred years investigators have speculated how the toothed whales could use this unique larynx to produce sound (Murie, 1871, and Turner, 1868). Vibration of the tissue folds and of the elongated arytenoid cartilages have both been considered. To the best of our knowledge, however, experimental data either to support or refute these hypotheses have never been published.

SOUND SIMULATION TESTS

A series of experiments using the excised larynx and two severed heads of *Stenella* and the head of a fresh specimen of *Tursiops* was carried out. The basic plan was to deliver a controlled flow of air at various pressures through the larynx and the heads to determine whether sound could be produced, and if so, to analyze its characteristics and measure the pattern with which it was radiated from the head. A block diagram of the instrumentation used during these tests is presented in Text-fig. 4.

To test the excised larynx of *Stenella*, a glass connector was inserted into the trachea and air delivered through it at a pressure of 1 to 2 psi and a flow of 10 to 15 liters per minute. The lips of the arytenoids were approximated by manipulation with forceps. This procedure re-



TEXT-FIG. 4. Block diagram of the instrumentation used for the sound simulation tests.

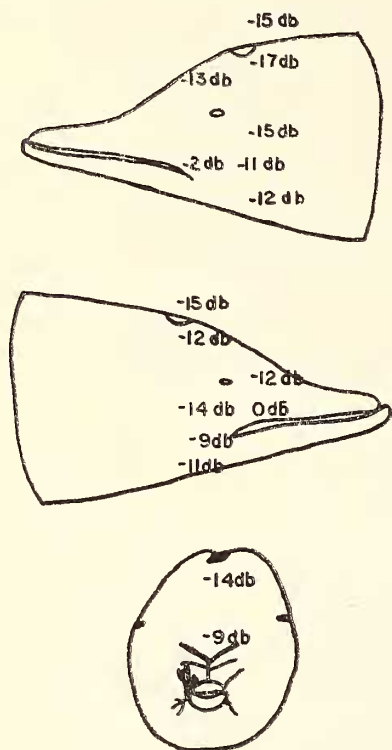
sulted in the production of a wide range of sounds depending on the amount of pressure applied and the proximity of the lips to each other.

Tests with the whole head required the same instrumentation as those with the excised larynx. To permit free access around the heads, they were suspended from a cross-arm with a glass connector inserted into the trachea. In this series of tests, no manipulation was used except to make certain that the aryteno-epiglottid tube of the larynx was well seated in the ventral openings of the bony nares. Sound was produced at pressures and flow rates of the same order of magnitude as those in the previous test with the larynx alone.

The sounds produced during both types of test were quite similar. Depending on the pressure applied and position of the larynx, sounds ranging from barks, rich in harmonics, to whistles were produced (Plate III, A & B). In

addition to these sounds, short duration pulse-type signals (Plate III, C), very similar to those employed in echo-location, were generated by air flowing through the nasal sac system of one specimen of *Stenella*. As air was forced into the excised heads, the blowhole became closed and the pressure was allowed to build up to two pounds per square inch. With the blowhole effectively sealed, the air sacs, especially the vestibular ones, would become inflated. Pressures inside the sacs, vestibular and premaxillary, were checked by inserting a spinal tap needle through the tissues into the sac. The core of the needle was then removed and a manometer attached. In the case of sounds similar to echo-location clicks, it was necessary for the sacs to be filled with air before any clicks were heard. If pressure was applied to the melon, for example by a hand pressed across the forehead, the sacs could be collapsed. Although the exact mechan-

Stenella Graffmani MLP 60-11 ♀ 69
 Ref: OASPL 93 db re: .0002 dynes/cm² (0 db)
 0.25 in. from head
 Airflow: 10 liters/mln
 1.04 lb/in²



TEXT-FIG. 5. Over-all sound pressure levels measured at various locations .25 inches from the head of a specimen of *Stenella graffmani* during sound simulation tests.

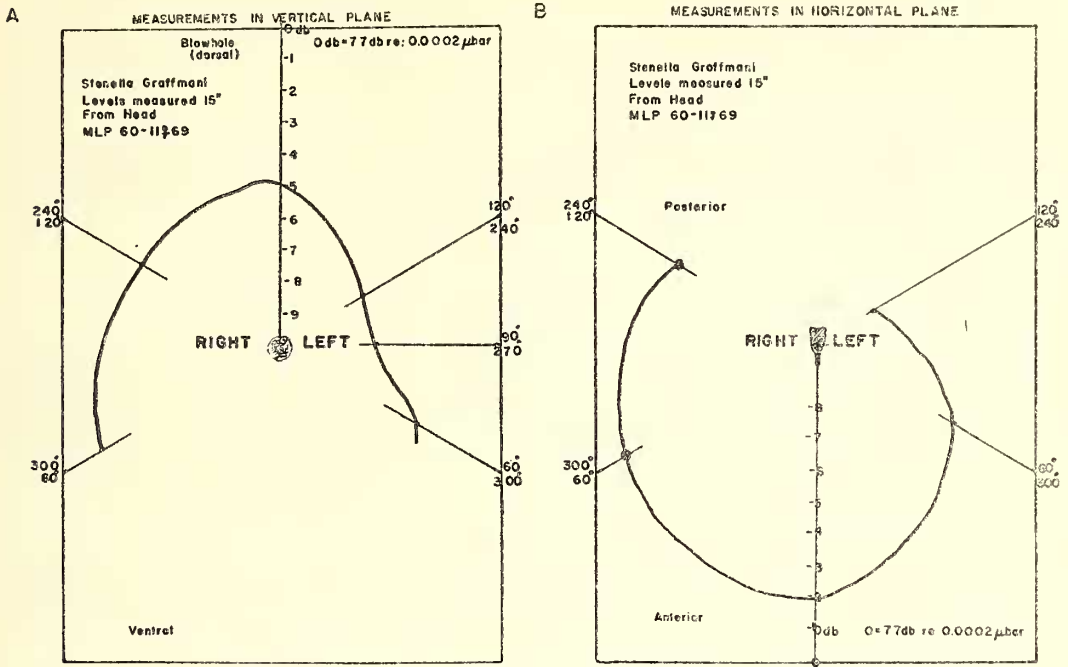
ism that produced these signals was not determined, deflation of the upper or distal nasal tract stopped the echo-location clicks. These sounds were achieved with air pressures of 1 psi within the specimens of *Stenella* and 1.5 psi within the *Tursiops*. Air flow was 10 liters per minute for both.

In addition to the sonographic analyses made of the clicks produced with the heads, measurements were also made of the over-all sound pressure level $\frac{1}{4}$ of an inch and 15 inches from the head at every 60° in the horizontal and vertical planes. The measures of over-all sound pressure level near the surface of the head at both distances are shown by the polar plots presented in Text-figs. 5 & 6. Most noteworthy is the asymmetrical radiation, with the stronger signal output on the right. This asymmetry immediately calls to mind the general asymmetry of cranial structures in toothed

whales (Odontoceti) noted by anatomists. Hosokawa (1950) has reported this in the musculature of the larynx of the sperm whale; Lawrence & Schevill (1956) have noticed this in the nasal sac system and skulls of *Tursiops truncatus* and *Stenella plagiodon*; and we have found that the nasal sacs in *Tursiops truncatus* and *Stenella graffmani* are larger on the right side. In fact, all the delphinids examined by the junior author have exhibited an asymmetrical development of the cranium and nasal sac system. These include *Delphinus bairdi*, *Tursiops gilli*, *Lagenorhynchus obliquidens*, *Stenella longirostris* and *Globicephala scammoni*.

The indirect evidence presented so far indicates that porpoises do have structures that can produce a variety of different types of sounds. It does not, however, add any support to the contention that echo-location clicks and whistling sounds are produced by separate mechanisms. The following observations, however, add credence to the supposition of specialized sound producers.

All of the initial observations of sound production using specimens of *Tursiops* were accomplished with groups of five or more animals. In order to simplify the sound analyses and observations on behavior, one animal was transferred to the smaller plastic-lined tank one day before testing. In this tank the porpoise was not restrained and was given food immediately. Using the previously described equipment, recorded *Tursiops* sounds, whistles and clicks were broadcast into the tank. Until this test, not a great deal of success had been achieved in eliciting whistles from solitary animals. During this test and for a period after stimulation, however, several long whistles were produced by the animal. The most interesting aspect of this behavior was that in all cases, the solitary animal produced echo-location signals and whistles simultaneously. Lilly & Miller (1961) report similar behavior from a physically restrained, solitary *Tursiops*. The time duration of the whistle portion of the simultaneous emissions that they observed ranged from .1 to .4 seconds. We have observed whistle durations from .45 to 1.5 seconds, the majority of them being longer than .6 second. Several sonagrams of these simultaneous signals are shown in Plate IV in which it can be seen that the whistles are overlaid on the pulsed signal. The whistles are not highly modulated and appear normal, that is, as they do in Plate I, B. If only one mechanism for sound production was involved, the whistle could be expected to show some of the modulations of the echo-location signal.



TEXT-FIG. 6. Over-all sound pressure levels measured every 60°, 15 inches from the head of a specimen of *Stenella graffmani* in both **A** vertical plane and **B** horizontal planes.

CONCLUSIONS AND SUMMARY

1. All of the natural vocalizations of a group of *Tursiops* and a single individual *Tursiops* can be placed in one of the three following categories: Plosive or pulse signals, whistles and barks.
2. Both *Tursiops truncatus* and *Stenella graffmani* have anatomical structures capable of producing a variety of sounds under conditions of artificial stimulation. These sounds are not unlike the ones produced naturally by these animals. Sounds artificially produced in the head of a specimen of *Stenella* showed an asymmetrical sound radiation pattern corresponding with the asymmetry of the cranial structures.
3. *Tursiops* is capable of producing echo-location pulses and whistles simultaneously.
4. Anatomical and behavioral evidence, as well as sound pressure measurements, indicate that the echo-location clicks are produced in the nasal-sac system of porpoises. Within the sac-system, the tubular sacs combined with the nasal plug nodes appear to be the site of sound production. It is only through the tubular and connecting sacs that we find a continuous air passage, the vestibular and pre-maxillary sacs being *cul de sacs*.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. Sonagrams of examples of the three types of sound produced underwater by *Tursiops truncatus*. A. Clicks or pulses. B. Whistle. C. Bark.

PLATE II

- FIG. 2. A. Larynx from *Stenella graffmani*. B. Larynx from *Tursiops truncatus*.

PLATE III

- FIG. 3. A. Sonagrams of sound produced by passing air through the excised larynx of *Sten-*

ella graffmani. B. Sonagrams of sound produced by passing air through a severed head from *Stenella graffmani*. C. Sonagram of short-duration, repetitive, pulse sounds generated by air flow through the nasal sac system of one specimen of *Stenella graffmani*.

PLATE IV

- FIG. 4. Sonagrams of four instances of simultaneous production of echo-location pulses and whistles by a single isolated *Tursiops truncatus*.